
SEQUENCING NEW WORLD ECOSYSTEMS: COMPARISON OF THE CRETACEOUS AND CENOZOIC APPEARANCE OF HABITATS WITH BIOME- CHARACTERIZING PLANT GROUPS¹

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ABSTRACT

Concepts about development of the plant component of New World terrestrial ecosystems through deep time have reached a point where it is possible to consider some subtle and refining details about the process. One such detail is the temporal relationship between the opportunity of new habitats provided by the physical processes of landscape development and long-term climate change, and the availability of the mostly angiosperm lineages that presently occupy these habitats. Some habitats (e.g., beach/strand/dune) were in existence long before the rise of the flowering plants ca. 125 million years ago (Ma), and some did not develop until late in the Neogene from a combination of cooling climates and locally to regionally increasing elevations (alpine tundra/páramo). In other instances, both habitats and lineages existed contemporaneously, but in different parts of the world, so development of the particular ecosystem had to await the appearance and spread in the New World of the lineage through migration (e.g., *Rhizophora* L. into modern mangrove habitats after the Late Eocene; *Quercus* L. from the north into modern oak–*Weinmannia* L. habitats only after 330 thousand years ago (Kyr). The temporal correspondence between opportunity and availability joins the more widely recognized forcing mechanisms of geologic and climate change, acting on evolutionary processes, as one additional factor in better understanding the origin, composition, and distribution of the ecosystems that presently characterize the New World.

Key words: Ecosystems, environments, Late Mesozoic, lineages, New World, Tertiary.

Sorting the events, processes, and chronologies involved in assembling New World ecosystems has reached a point where broad summaries are forthcoming that serve as a baseline for incorporating new discoveries and fine-tuning existing scenarios. The term “ecosystem” as used here refers to the living envelope or biome, climate, and geological features such as soils and topography that have interacted over time to produce recognizable segments of the Earth’s landscape—e.g., tundra, boreal forest, desert, grasslands, deciduous forest, mangroves, and rainforest. Summaries have been compiled for major geographic regions such as North America (e.g., Graham, 1999), the West Indies (Woods & Sergile, 2001), Amazonia (Hoorn & Wesselingh, 2010; Hoorn et al., 2010), and Latin America (Graham, 2010a); others treat specific ecosystems such as tropical montane cloud forests (Churchill et al., 1995; Kappelle & Brown, 2001; Bruijnzeel et al., 2010) and the tropical rainforest (Morley, 2000), while others attempt broader histories for the New World intended for a general audience (Graham, 2010b,

2011). These summaries provide an opportunity to refine details in that history.

Most of the Earth’s modern biomes have a prominent angiosperm component so this identifies the Middle to Late Cretaceous as a convenient starting point because after an origin in the Early Cretaceous to possibly the Late Jurassic, flowering plants began to diversify and radiate to become the characteristic element of most present vegetation. The approach here and in other publications by Graham (1999, 2010a, 2010b) has been to 1) identify the principal changes in geology (i.e., physical, topographic histories) and climatic environments that shaped the evolution of ecosystems in the Americas from about the Middle and Late Cretaceous (ca. 100 million years ago [Ma]) to the end of the Pliocene (ca. 2.6 Ma); 2) compile inventories of representative plants for each of the modern ecosystems, indicating which plants were present in the plant fossil record for the region and for this interval (Appendix 1); 3) track the progression of ecosystem development from the appearance of individual elements, through early versions, to essentially modern versions of the

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communities (Graham, 2010b: table 7.1, 2011), and now as an additional refinement; and 4) compare the appearance of habitats with the appearance of lineages available to occupy these habitats that together helped shape the versions of the ecosystems present today.

GEOLOGIC AND CLIMATIC ENVIRONMENTS

In the Cretaceous the initial separation of South America from Africa started in the south at ca. 120 Ma and reached the north coasts of the continents ca. 100–90 Ma. Atmospheric CO₂ concentration in the Maastrichtian was ca. 1000 parts per million by volume (ppmv), probably not exceeding 1300 ppmv, and global mean annual temperatures (MATs) were ca. 11.2°C warmer than at present (Andrews et al., 1995). There were equable maritime climates, high sea levels, extensive epicontinental seas, flooded coastlines, low pole-to-pole thermal and biodiversity gradients with little evidence of significant or sustained glaciers, broad continental connections, and widespread distribution of many plant and animal species. At the Cretaceous/Tertiary boundary ca. 65 Ma, the asteroid impact (Nichols & Johnson, 2008) caused extinction of up to 50% of all species (more among the marine plankton) and altered the reptile (predator)–mammalian (prey) balance and other evolutionary dynamics. There was a slight and temporary lowering of global temperatures from ash that blocked sunlight, followed by rising temperatures from increased CO₂ and other greenhouse gas concentrations (Beerling, 2007) but with no long-term effect on climate (Crowley & North, 1991); and possibly some selection toward deciduousness. In the Middle and Late Cretaceous (ca. 100–70 Ma), the epicontinental seas and coastal waters began to retreat due to the uplift of continents and decreased formation of submerged, water-displacing plateaus. Temperatures cooled by ca. 4°C (Zachos et al., 2008) as CO₂ out-gassing waned from the slowing of plate motion, and South America separated from North America. In the Late Paleocene/Early Eocene (ca. 55 Ma), a sudden increase in atmospheric CO₂ concentration (Sexton et al., 2011) to ca. 1300–1600 ppmv occurred, possibly involving emission from explosive vents in the Norwegian Sea as Greenland separated from Europe, and there was a further increase in MAT, perhaps as much as 5°–6°C in the equatorial regions (Head et al., 2009). An early version of the lowland Neotropical rainforest reached its maximum extent from an origin ca. 58–55 Ma (Wing et al., 2009), and tapir, crocodile, and Musaceae (banana-like) lineages extended to within the Arctic Circle.

From these peaks in temperature, moisture, and distribution of tropical vegetation, the atmospheric CO₂ concentration declined, ranging from 1000 to 1500 ppmv between 34 and 24 Ma (Middle to Late Eocene; Pagani et al., 2009), and temperatures began an episodic descent from the hothouse interval of the Paleogene into the icehouse times of the Neogene.

Between 49 and 44 Ma (Middle Eocene), spreading along the mid-Atlantic Ridge reached the North Atlantic disrupting the land bridge between North America and Europe at about the same time as temperatures began to cool. During this interval the proto-Greater Antilles emerged as an eastward-moving volcanic island arc that was colliding with the Bahamas Platform. Around 40 Ma the Rocky Mountains and the Andes Mountains were in an early period of uplift, and at 32 Ma South America separated from Antarctica to become an island continent. This initiated the cold Humboldt Current that began cooling the west coast of South America. Continental glaciation began on Antarctica near the Eocene/Oligocene boundary ca. 34 Ma (Bo et al., 2009), and a drop in temperature at the end of the global Middle Miocene Climatic Optimum (MMCO) initiated alternating full-scale glacial and interglacial fluctuations on Antarctica at ca. 17 Ma (Andrill Antarctic Geologic Drilling Project of the sea floor, McMurdo Sound, <<http://www.andrill.org>>). Between ca. 10 and 6 Ma, the Andes Mountains attained the near-final half of their present maximum height, rising from an average of 2000 to 4000 m (Oncken et al., 2006; Graham, 2009a, 2010a: 88–97, 2010b: 76–88). Around 5–3 Ma there was a Pliocene warm period and although sea levels may have risen by ca. +20 m (<<http://www.andrill.org>>), uplift and accumulating volcanics in present-day southern Central America reunited South America with North America through formation of the Isthmian Land Bridge at ca. 3.5 Ma. Widespread continental glaciations began in the Quaternary, which was recently defined by the International Commission on Stratigraphy and the International Union for Quaternary Research as beginning 2.6 Ma (see Giles, 2005).

These physical and climatic events acting on evolutionary processes within lineages resulted in a sequence of ecosystems beginning with eight versions recognized for the Cretaceous. These were 1) the polar broad-leaved deciduous forest, 2) notophyllous broad-leaved evergreen forest, 3) paratropical rainforest, 4) tropical forest, 5) aquatic, 6) herbaceous freshwater bog/marsh/swamp, 7) mangrove, and 8) beach/strand/dune. One hundred million years later, events and processes have resulted in the 12 versions

currently recognized for the New World. These are 1) desert, 2) shrubland/chapparal-woodland-savanna, 3) grassland, 4) mangrove, 5) beach/strand/dune, 6) freshwater herbaceous bog/marsh/swamp, 7) aquatic, 8) lowland Neotropical rainforest, 9) lower to upper montane broad-leaved forest (deciduous forest), 10) coniferous forest, 11) alpine tundra (páramo), and 12) tundra. The terminology, composition, proposed developmental sequence, and chronology of this transformation have been discussed earlier (Graham, 1999, 2010a, 2010b, 2011). The inventories on which they are based are included in the tables and appendices of Graham (1999, 2010a), respectively, and representatives are given in Appendix 1.

INVENTORIES

After reviewing the geologic and climatic events contributing to the development of New World ecosystems the next step is to compile the representative plant genera that characterize the 12 modern ones (Graham, 1999, 2010a, cf. references). The last step logically would be to consult an inventory of Cretaceous and Tertiary plants for the region. Ideally, the entries would have been assessed for accuracy of the age, locality, and identification of the specimens, and would include the relevant literature and location of the types. Although compilations of the fossil record for individual genera and families are available (e.g., Juglandaceae, Manos et al., 2007; Rubiaceae, Graham, 2009b; Lythraceae, S. Graham, in prep.), no overall database exists. New discoveries rapidly render printed summaries of plant family histories, phylogeny, and biogeography obsolete even when published only shortly before (e.g., for the Lythraceae, S. Graham, personal communication, 2011). Several electronic and printed versions have been attempted (see Graham, 2010a: xiii) and others are underway, including a catalog of Cretaceous and Cenozoic vascular plants for the New World (<<http://www.mobot.org/mobot/research/CatalogFossil/catalog.shtml>>; see Graham, 2012, in this issue), but it will be a long time before a dependably complete inventory is available. In the meantime, prominent genera in the plant biome that are part of modern New World ecosystems and their fossil representation (based on Graham, 1999, 2010a: app. 1 and 2, and references cited therein) are presented in Appendix 1. This compilation allows only a shadowy insight into the correspondence between habitat opportunity and the appearance of lineages suitable to occupy those habitats. Experience has shown that it will be tempting to use the partial inventories and new discoveries of fossil

plants to prematurely reinvent such concepts as tropical rainforest and environmental dynamics, the history of northern temperate elements in the Latin American biota, leaf/climate relationships, closure of the isthmian land bridge, and refugia. Even so, and even with the limitations of the database in its present state, the records currently allow refinements in the history of the plant component of New World ecosystems. As the inventory improves, a sharper image of this history is emerging.

ECOSYSTEM DEVELOPMENT

The sequence of appearance of Cretaceous and Tertiary ecosystems in the New World has been summarized in Graham (2010b: 174–198, 209–228, 235–267, 275–299, table 7.1; 2011). Elements (E in table 7.1) of most ecosystems appeared in the Cretaceous and Paleogene, but they coalesced into early versions (EV) and then into essentially modern versions (EM) in the Cretaceous (e.g., aquatic communities, lower to upper montane broad-leaved forests), Paleogene (coniferous forest, lowland Neotropical rainforest, modern New World mangroves), during and just after the MMCO (widespread grasslands, tropical dry forests, and related vegetation types), and in the Middle Miocene and Pliocene (deserts, lowland tundra, alpine tundra, or páramo). An influencing factor and another detail in this gradational development was the subtle, but nonetheless recognizable, interaction between the appearance of suitable habitats and the appearance of modern lineages to occupy these habits, allowing definition of the present-day ecosystems.

HABITAT OPPORTUNITIES AND LINEAGE AVAILABILITY

Some lineages defining the plant formations and associations of the New World ecosystems coevolved in concert with the relatively recent appearance of local to regional suitable habitats (e.g., *Lupinus* L., Hughes & Eastwood, 2006; *Polylepis* Ruiz & Pav., Simpson, 1986; the parrot genus *Pionus*, Ribas et al., 2007) in the Andean Highlands. Other progenitors were likely introduced periodically via migration and persisted when and if suitable habitats appeared. The subject of this study is to examine approximately when, for example, did *Betula* L. and *Acer* L./*Quercus* L. and *Juglans* L. (in eastern North America); *Pinus* L. and *Quercus* (Mexico, northern Central America); *Quercus* and *Weinmannia* L. (highlands of Colombia); Poaceae (mid-continent North America, central Argentina); *Rhizophora* L. (tropical and warm-temperate coasts); *Pinus–Picea* A. Dietr.–*Abies* Mill.–*Tsuga*

(Endl.) Carrière—*Alnus* Mill.—*Betula*—*Populus* L.—*Salix* L. (mountains of northwestern North America); *Decodon* J. F. Gmel.—*Cabomba* Aubl.—*Nymphaea* L.—*Pachira* Aubl.—*Trapa* L.—*Typha* L. (various aquatic habitats); and genera that would eventually form the lowland Neotropical rainforest come together to constitute the present-day beech-maple/oak-hickory associations of the deciduous forest formation; the pine-oak association of the mid-altitudes of northern Latin America; the oak—*Weinmannia* woods of the Andean forest belt of Colombia; the grasses of the prairies and pampas; the modern *Rhizophora*-dominated mangrove communities; the coniferous and boreal forests of the high altitudes and latitudes; aquatic communities with a prominent angiosperm component; and the modern rainforest? That is, what was the temporal relationship between the physical opportunity provided by geologic and climatic events (namely, the presence of suitable habitats) and the availability of lineages to occupy those habitats as a development in defining modern New World ecosystems? Aquatic and brackish-water coastal conditions were available long before the Cretaceous; dry to arid seasonal habitats developed extensively during and after the MMCO; and cold, high-altitude environments appeared in the Mio-Pliocene and Quaternary when the later phases of Andean and other mountain uplift combined with cooling trends in the Neogene. However, *Rhizophora* did not appear in the New World until the beginning of the Middle Eocene; many northern temperate deciduous elements, present since the Late Cretaceous and Paleogene in the high latitudes, did not move south in significant numbers to modernize the temperate forests of northern Latin America until the decline in temperature after the MMCO; and although *Quercus* is known from North America since the Late Cretaceous, it did not appear in northern South America until about 330 thousand years ago (Kyr) to form the modern oak—*Weinmannia* community of the upper Andean forest. This study explores the temporal correspondence between habitat opportunity and lineage availability as suggested in Appendix 1, even as it presently stands, as one factor in conceptualizing the sequence of development of modern New World ecosystems.

AQUATIC AND FRESHWATER HERBACEOUS BOG/MARSH/SWAMP

These habitats have been available since the origin of the lithosphere and were ready for colonization by angiosperms whenever they appeared (ca. 125 Ma or before). Aquatic and other freshwater environments were already occupied by a variety of angiosperm families in Early Cretaceous and Paleocene times; hence, they are among the oldest essentially modern

(namely, angiosperm-dominant) versions of present-day ecosystems. This is not unexpected given that wetland/aquatic seasonally unpredictable habitats, along with fluctuating dry sites in West Gondwana, are considered places of origin and/or early differentiation of the flowering plants. From Appendix 1 it is seen that Cretaceous and Paleogene lineages available in the New World that took advantage of this habitat opportunity were the Araceae (*Pistia* L.), Cabombaceae (*Brasenites*, extinct), Ceratophyllaceae (*Ceratophyllum* L.), Haloragaceae (*Obisopocaulis*, *Tarahumara*, both extinct), Lemnaceae (*Limnobiophyllum* extinct), Lythraceae (*Decodon*, *Trapa*), Nymphaeaceae and plants with nymphaealean affinities (*Aquatifolia*, *Paranymphaea*, *Pluricarpaella*, all extinct), Trapaceae (now part of Lythraceae; *Hemitrapa*, extinct; note that *Trapa* in pre-Miocene North American floras [e.g., Barnett, 1989] may be *Hemitrapa*; the paleocomplex of related/similar genera needs revision; S. Graham, personal communication, 2011), incertae sedis: *Iara* (extinct), *Quereuxia* (extinct, *Trapago*); several probable aquatics from the Lower Cretaceous Crato Formation of Brazil (Mohr & Friis, 2000); in addition to the Azollaceae—*Azolla* Lam. and other older fern and allied groups. The related freshwater herbaceous bog/marsh/swamp habitat was early occupied by *Sphagnum* L., *Selaginella* P. Beauv., *Equisetum* L., and various ferns, but the record of early angiosperms in this environment is not well known.

BEACH/STRAND/DUNE

This is another ancient habitat, but because conditions for preservation are poor in the coarse, shifting sand environment, the history of the ecosystem is not well known. The earliest New World records for the Aizoaceae (a family that includes, e.g., the extant *Sesuvium portulacastrum* (L.) L.), Amaranthaceae (*Iresene* P. Browne), Batidaceae (*Batis maritima* L.), Convolvulaceae (*Ipomoea pes-caprae* (L.) R. Br.), Fabaceae (*Canavalia maritima* Thouars), Poaceae (*Uniola paniculata* L.), Polygonaceae (*Coccoloba uvifera* (L.) L.), and others that can range into the habitat may extend back into the Cretaceous (e.g., Fabaceae) and Paleocene (Poaceae), but fossil records for these genera are unknown or are comparatively recent, probably due, in part, to taphonomy.

LOWER TO UPPER MONTANE BROAD-LEAVED FOREST (LATIN AMERICA)/DECIDUOUS FOREST (EASTERN NORTH AMERICA)

Terrestrial habitats extending from the coast to the moderate Cretaceous and Paleocene highlands were

available in the Cretaceous and were soon occupied after 125 Ma by a version of this ancient ecosystem. It has an extensive representation in the fossil record (Appendix 1). Present in the Cretaceous and Paleocene were Aceraceae (possibly *Acer*; oldest record Late Cretaceous, Hell Creek Formation, South Dakota; see reference to Kirk Johnson's ongoing study noted in Renner et al., 2008), Araucariaceae (*Araucaria* Juss.; extinct organ genera *Araucariopitys*, *Araucarioxylon*, *Araucarites*), Atherospermataceae (Laurales; *Laurelia*, extinct), Betulaceae (*Betula*; oldest record Middle Eocene Allenby Formation, British Columbia, Canada; Crane & Stockey, 1987), Carpinaceae (*Carpinus* L.–*Ostrya* Scop., as pollen), Ebenaceae (*Diospyros* L.), Ericaceae (*Andromeda* L.), Fagaceae (*Nothofagus* Blume, *Quercus*; *Quercinium*, extinct), Fagaceae s.l. (*Antiquacupula*, *Protofagaceae*, both extinct), Ginkgoaceae (*Ginkgo* L.), Hamamelidaceae (*Allonia*, extinct), Lauraceae (*Persea* Mill. type), Magnoliaceae (*Magnolia* L.), Malvaceae (*Javelinoxylon*, extinct), Platanaceae, Podocarpaceae (*Dacrydium* Lamb., *Podocarpus* L'Hér. ex Pers.; *Gamerroites*, *Podocarpidites*, both extinct), Taxaceae (*Acmopyle* Pilg.), Taxodiaceae (*Glyptostrobus* Endl., *Metasequoia* Hu & W. C. Cheng; *Athrotaxites*, *Taxodioxygen*, both extinct), Theaceae (as *Ternstroemia*, extinct, Early Eocene), Tiliaceae, Ulmaceae (*Ulmus* L.); in addition to *Adiantum* L., *Blechnum* L., *Dennstaedtia* Bernh., *Dryopteris* Adans., *Gleichenia* Sm., *Hymenophyllum* Sm., *Thyrsopteris* Kunze, and other older fern and allied groups that can occur in this community.

LOWLAND NEOTROPICAL RAINFOREST

The physical factors supporting this biome are a low-lying elevation generally less than 900 m, high water table, relatively level terrain so slope and exposure do not cause rapid removal of water, and rapid mineral recycling resulting in soils sterile at depth. The climate factors are a high and relatively uniform temperature (MAT ca. 24°C with the coldest-month mean at least 18°C), and high and relatively uniform mean annual precipitation (MAP) of ca. 1500–1800 mm to a maximum of 11,000 mm with the driest four months receiving at least 18% of the annual rainfall; if MAP falls below ca. 1500–1800 mm, the vegetation trends toward dry forest and savanna. The question is when did these physical and climatic factors first develop over an extensive area in the New World to provide the physical opportunity for development of a recognizable lowland Neotropical rainforest?

By ca. 100–90 Ma, northward spreading along the Mid-Atlantic Ridge had reached the vicinity of

northwestern Africa–northeastern South America and the two continents began to fully separate (Veblen et al., 2007). This disrupted the vast continental interior of West Gondwana and was followed by marine inundation of the proto-Amazonian lowlands. Deposition of the Late Cretaceous limestone substrate (Wanderley-Filho et al., 2010) constituted much of the floor and defined the initial underlying topography of the basin. Early uplift of the Northern Andes began draining the basin and isolating the Amazon and Solimões sub-basins in the Cretaceous–Paleogene. This was followed by periodic and partial marine inundation of riverine and lacustrine freshwater habitats during the Tertiary with reversal of the Amazon and Orinoco rivers from west into the Pacific to east into the Atlantic in about the Middle Miocene (ca. 15 Ma; Hoorn & Wesselingh, 2010). Thus, the Early Paleogene (ca. 60 Ma) was a suitable time in terms of physical habitat for beginning the development of an extensive lowland Neotropical rainforest in the New World. This was also a time of climatic warmth and moisture that would culminate with the Early Eocene Climatic Optimum (EECL) ca. 55 Ma.

Elements of a rainforest were present in the earliest Paleocene in places like Colorado (64 Ma; Elaeocarpaceae, Lauraceae, Sterculiaceae) and many had a leaf physiognomy typical of tropical species (entire margins, drip tips), but composition-wise this flora also included lineages that presently are primarily temperate like Platanaceae and Tiliaceae (Johnson & Ellis, 2002). The consensus is that an ecosystem representing an early version of rainforest first began assembling over an extensive area in the New World between ca. 58 and 55 Ma (Burnham & Graham, 1999; Burnham & Johnson, 2004; Wing et al., 2009). A lowland Neotropical rainforest was able to take shape because several angiosperm plant groups were adapted or were adapting to tropical conditions and were present to take advantage of the opportunity provided by the geologic and climatic events and trends (Appendix 1). These included Actinidiaceae (*Parasaurauia*, extinct)/Araceae, Arecaceae, Fabaceae, Malvaceae, Menispermaceae, and Zingiberales (Wing et al., 2009); Elaeocarpaceae and Sterculiaceae (Johnson & Ellis, 2002); and Lauraceae (*Mauldinia*, extinct; family level: Johnson & Ellis, 2002; Wing et al., 2009).

CONIFEROUS FOREST

Although gymnosperms were prominent in the pre-Early Cretaceous vegetation and remained intermingled with angiosperms, usually in diminishing numbers and kinds after the flowering plants rose

to dominance (Graham, 2010a: 374), coniferous gymnosperms forming a forested modern ecosystem did not appear until later. The varied factors combining to produce habitats allowing conifers to compete favorably and persist amidst the diversifying and radiating angiosperms are discussed in Graham (1999: 8). The climatic factor included globally cooling temperatures just after the EECL, augmented regionally by the physical factor of increasing elevations. Uplands further resulted in greater moisture stress (physiological aridity) by runoff/evaporation from slope and exposure to which gymnosperms are morphologically and physiologically adapted (sunken stomata, tannin-containing cell vacuoles). A time and place in which the physical factors early combined to make extensive habitats available for the development of a coniferous forest ecosystem was ca. 49–48 Ma in the Northern Rocky Mountains regions as represented by the Republic Flora of northeastern Washington. Here *Abies*, *Chamaecyparis* Spach, *Picea*, *Pinus*, *Pseudolarix* Gordon, *Thuja* L., *Tsuga*, and the oldest definite *Betula* from the Middle Eocene Allenby Formation, British Columbia, Canada (Crane & Stockey, 1987), combined to produce a western montane association of the coniferous forest formation. This association spread into lowlands to form a boreal forest, and in the highlands farther south as an alpine forest just below timberline, beginning with cooling after the EECL and especially in Oligocene and later Neogene times.

The lineages available already in the Late Cretaceous and Paleocene, or that soon coevolved to take advantage of this habitat opportunity (Appendix 1), were *Abies*, *Picea*, *Pinus*, *Tsuga*, possibly “*Acer arcticum*” of the aff. *Aceraceae* complex, and *Betulaceae* (*Betula*) from several Late Cretaceous and Paleocene sites (e.g., Graham, 1999: 162, et seq.).

MANGROVE

Coastal and river inlet brackish-water, tropical to warm-temperate habitats are ancient and in the Late Cretaceous through about the Middle Eocene they were occupied by ferns (e.g., spores of cf. *Acrostichum* L., mangrove fern), palms (*Nipa* Thunb.), and a plant of unknown biological affinities producing pollen called *Brevitricolpites* abundant in pre-Middle Eocene tropical low-lying coastal deposits. However, the plant that presently characterizes much of the New World mangrove ecosystem, *Rhizophora*, did not appear until about the beginning of the Late Eocene (Graham, 1995; 2010a: 489–490, and references therein) and this dates the earliest, essentially

modern, version of mangrove vegetation in the Americas at ca. 34 Ma.

GRASSLANDS

The presence of extensive grass-dominated ecosystems such as prairie and pampas has had a long attenuated history (Graham, 2010b: 33–37). Physical conditions suitable for the eventual development of grasslands began with the retreat of the epicontinental sea from mid-continent North America in the Middle to Late Cretaceous. This left a limestone substrate weathering into calcareous soil favorable for the growth of grasses. The rise of the Rocky Mountains to heights sufficient to create a rain shadow in the mid-continent region toward the end of the Eocene (possibly earlier locally) was a second factor. This reduced precipitation, but low pressure systems from the Gulf of Mexico provided some moisture, so conditions were too dry for extensive forests but too wet for deserts. As grasses increased in prominence, fire became an increasingly important reinforcing event. Climate was a culminating factor because by the Middle Miocene (ca. 17–13 Ma) cooling had reached a point where reduced evaporation from ocean surfaces created widespread drying and greater seasonality. This was when elements began to increasingly coalesce into early versions of grasslands and communities of dry aspect.

The earliest evidence of grasses are phytoliths from Late Cretaceous coprolites of India (Piperno & Sues, 2005; Prasad et al., 2005), and in the New World from the Early Eocene of Tennessee (Crepet & Feldman, 1991; Graham, 1999: 170, 2010a: 261). The northern grassland as an extensive, recognizable ecosystem comes into its own, however, only about and just after the Mid-Miocene drying with the gradual decrease of forests. The Palouse Prairie to the west of the Rocky Mountains in Oregon developed ca. 3 Ma when the rise of the Cascade Ranges created drying to the lee side. The pampas of Argentina as a distinct, recognizable community developed in response to the rise of the Southern and Central Andes and also to the global trend toward drying and deciduousness in and after the Middle Miocene. It is also located under the descending arm of the Hadley atmospheric circulation cell. These are also factors in the presence of the monte and Gran Chaco located between ca. 20° and 40°S latitude (Graham, 2010a: 42–44).

SHRUBLAND/CHAPARRAL—WOODLAND—SAVANNA AND DESERT

Evidence from geology (increasing slope, exposure, rain shadows, paleosols), and climate (cooling

temperature, increasing dryness, greater seasonality) provides a context for comparing the opportunity provided by increasing dry habitats with the availability of dry-adapted lineages. This evidence supports the intuitive assumption that dry to arid ecosystems would appear at about the same time as grasslands and fully develop somewhat later in the Neogene with increasing dryness (Graham, 1999: 266–268, 2010a: 261–262). Progenitors were present as individual elements and local early versions by the Middle Eocene (e.g., Green River Flora, Colorado/Utah, ca. 45 Ma; *Ephedra* L. throughout the Americas), but soils, landscape, and climate combined to produce extensive, essentially modern versions in the Middle Miocene and especially in Late Miocene and Pliocene. It is also evident from Appendix 1 that fewer genera characterizing distinctly drier vegetation are present in the Cretaceous and Paleocene floras than in the vegetation types previously discussed, and those in the later Paleogene often represent wide-ranging taxa found in other habitats (e.g., *Acacia* Mill., *Aesculus* L., *Ilex* L., *Jacaranda* Juss., *Pinus*, *Quercus*). The families were present, but the genera forming the shrubland/chaparral–woodland–savanna mostly came later and coalesced in the Neogene. True deserts become most evident and most extensive in the plant fossil record during the Late Miocene/Pliocene and during the interglacials of the Quaternary.

The concept of a Neogene origin for modern deserts is the contribution primarily of Daniel Axelrod (1950, 1979, 1983). An essential component of that concept is that the rise of the western mountains, particularly the Sierra Nevada, to heights sufficient to create rain shadows to the lee side is a relatively recent event. The assumption is currently being debated and higher elevations earlier in the Cretaceous and Tertiary are being proposed (Dokka & Ross, 1995; Wernicke et al., 1996; Wolfe et al., 1997; House et al., 1998; Poage & Chamberlain, 2002; Retallack et al., 2004; Stock et al., 2004; Mulch et al., 2006; Schuster et al., 2006). This emphasizes the need to conceptualize the development of modern ecosystems as typically gradational and that concept is facilitated by the device of recognizing elements, early versions, and essentially modern versions appearing over time.

TUNDRA AND ALPINE TUNDRA (PÁRAMO)

This is the last physical and climatic environment to appear extensively in the New World. Tundra habitats depended on the culmination of the Neogene cooling trend in the Late Pliocene (5–3 Ma) and in

the Quaternary beginning ca. 2.5 Ma, and alpine tundra/páramo, additionally, upon the elevation of highlands toward their maximum altitudes. Asteraceae, Cyperaceae, Ericaceae, Fabaceae, Juncaceae, Poaceae, Rosaceae, and others appeared long before the Neogene, but the physical and climatic conditions were local and late in coming and the lowland and alpine tundra, along with modern deserts, are the most recent of the Earth's ecosystems to appear.

Refining the details of the origin and history of New World ecosystems has become possible only after the broad outlines of geologic, climatic, and biotic events and processes were established (Graham, 1999, 2010a, 2010b, and references therein). In my later summaries culminating this particular series of studies, two such details have been considered: 1) the broad and overlapping sequence of appearance of the ecosystems (Graham, 2011); and 2) the correspondence between the appearance of habitats, and the presence of lineages to occupy these habitats, which further defines the sequence (present paper).

The latter observation adds a nuance to concepts about ecosystem origin and evolution. It capitalizes on the baseline data consisting of identifications, integration with results from other lines of inquiry, and interpretation within the broadest context of ancillary information (namely, a systems approach; Graham, 2010b: 2–5). A guesstimated 95% or more of ecosystem evolution is determined by the forcing mechanisms of geologic events and climatic change acting on evolutionary processes. It is suggested here that a small but significant refinement additionally involves the correspondence between opportunities for colonization provided by physical alterations in the environment and the fortuitous availability of lineages resulting from the random processes of evolution and dispersion.

In compiling this information it became evident that considerably better databasing of the paleobotanical record is needed. In Appendix 1 an asterisk (*) or double-asterisk (**) designates the genus or at least the family is reported in the fossil record. The others are characteristic genera of the ecosystems, and establishing a record for them would be especially useful in further clarifying lineage histories and paleoenvironmental reconstructions. Even in the present state of knowledge, however, it is evident that various habitats were available long before there were angiosperm lineages to occupy them (aquatic, freshwater herbaceous bog/marsh/swamp, beach/strand/dune). At other times the potential lineages or progenitors were present before there were suitable topographic and climatically defined habitats for

them to coalesce and expand (grassland, shrubland/chaparral–woodland–savanna in the Mid-Tertiary; tundra, alpine tundra/páramo in the Late Tertiary and Quaternary). In still other instances both habitats and genera were available but in different parts of the world, and formation of the modern ecosystem had to await migration (e.g., *Rhizophora* into the Americas, and *Quercus* into South America; the invasives of their time). Continuing alpha-level investigations (namely, the discovery of new fossil floras and revision of existing ones), improving geologic and paleoclimatic context, and refinements in the details (Little et al., 2010; Luna-Vega & Magallón, 2010; Manchester & O’Leary, 2010; Martínez-Millán, 2010), including the one discussed here, continue to provide an increasingly clearer picture of the Earth’s past and present ecosystems.

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APPENDIX 1. Modern plant genera prominent in New World ecosystems with emphasis on those known from the fossil record. Some genera range through more than one vegetation type or community association (in boldface). Extensive lists of certain taxa (e.g., grasses) are not included because individual genera usually cannot be recognized from fossils (Geisler, 1945). Genera indicated (*) are those reported from the Cretaceous and/or Tertiary of the New World. Similarly, families marked (**) represent where generic identifications of macrofossils are uncertain, or where generic distinction among microfossils is difficult (Cyperaceae, Poaceae, Amaranthaceae–Chenopodiaceae, noted as chenoam, Ericaceae, etc.). A single dagger (†) designates an extinct taxon. References to records include Graham (1999: tables and index, 2010a: app. 2, 2010b, 2011), Dillhoff et al. (2005) (Early–Middle Eocene, British Columbia, Canada), Falcon-Lang and Cantrill (2001, Middle Cretaceous, Antarctica), and Hoffman and Stockey (1999, Late Paleocene, Alberta, Canada). The oldest family records are designated as Cretaceous or Paleocene, e.g., **Haloragaceae, Cretaceous, Mexico. Identifications may include cf. affinities or form-type designations, e.g., *Ambrosia* L. type. For Quaternary records, see Graham (1999, 2010a).

DESERT, SHRUBLAND/CHAPARRAL–WOODLAND–SAVANNA

Many putative taxa (*) come from the Mid- to Late Tertiary and from midden remains of Quaternary age.

NORTH AMERICA (INCLUDING MEXICO)/ANTILLES/CENTRAL AMERICA

Acacia* Mill., *Achyranthes* L. (chenoam), *Acidoton* Sw., *Adenostoma* Hook. & Arn., **Aesculus* L., *Agave* L., **Ame-lanchier* Medik., **Amorpha* L., **Arctostaphylos* Adans., *Asteraceae* (**Ambrosia* L./*Franeria* Cav., **Artemisia* L.), **Astronium* Jacq., **Baccharis* L., *Beaucarnea* Lem., *Bejaria* Mutis ex L., **Berberis* L., **Brahea* Mart. ex Endl., *Bromelia* L., *Brosimum* Sw., *Brya* P. Browne, **Bucida* L., **Bursera* Jacq. ex L., *Byrsonima* Rich. ex Kunth, Cactaceae (*Carnegiea* Britton & Rose, *Cephalocereus* Pfeiff., *Cereus* Mill., *Echinocactus* Link & Otto, *Echinocereus* Engelm., *Ferocactus*, *Lemaireocereus* Britton & Rose, *Mammillaria* Haw., *Myrtillo-cactus* Console, *Neobuxbaumia* Backeb., *Opuntia* Mill., *Pachycereus* (A. Berger) Britton & Rose, **Pereskia* Mill.), **Caesalpinia* L., **Calliandra* Benth., **Capparis* L., **Cardiospermum* L., **Casearia* Jacq., **Cassia* L., **Ceanothus* L., **Cedrela* P. Browne, **Celtis* L., **Cercidium* Tul., **Cercocarpus* Kunth, **chenoam (*Amaranthus* L., *Atriplex* L., *Chenopodium* L., *Suaeda* Forssk. ex J. F. Gmel.), *Chrysobalanus* L., *Chrysothamnus* Nutt., **Coccoloba* P. Browne, **Comocladia* P. Browne, **Condalia* Cav., **Copaifera* L., *Coulterella* Vasey & Rose, **Crataegus* L., **Crescentia* L., **Croton* L., **Cupania* L., *Curatella* Loefl., *Cyrtocarpa* Kunth, **Dalbergia* L. f., **Dalea* L., **Daphnopsis* Mart., *Dasyllirion* Zucc., *Encelia* Adans., **Enterolobium* Mart., **Ephedra* L., ***Ericaceae* (**Arbutus* L., **Arctostaphylos*), *Erythea* S. Watson, **Erythroxylum* P. Browne, *Eugenia* L. (microfossils as **Eugenia*/*Myrcia* DC., with other genera of the family having similar pollen; Graham, 1980), **Euphorbia* L., *Flourensia* DC., **Fouquieria* Kunth, **Guetarda* L., *Haematoxylum* L., **Haplorhus* Engl., *Hechtia* Klotzsch, **Holodiscus* (K. Koch) Maxim., **Hymenaea* L., *Idria* Kellogg, **Ilex* L., *Ipomoea* L., **Iresine* P. Browne, **Jacaranda* Juss. (widespread), **Jatropha* L., *Juliania* La Llave & Lex., **Juniperus* L., *Kalmia* L., **Karwinskia* Zucc., *Koeberlinia* Zucc., *Lachnocaulon* Kunth, **Laetia* Loefl. ex L., **Larrea* Cav., *Leucophyllum* Humb. & Bonpl., **Lithocarpus* Blume, **Lysiloma* Benth., **Mahonia* Nutt., cf. **Malpighia* L., *Microcycas* (Miq.) A. DC., **Mimosa* L., *Nolina* Michx., *Olneya* A. Gray, *Parkinsonia* L., *Parthenium* L., **Persea* Mill., **Phyllanthus* L., *Pictetia* DC., *Pieris* D. Don., **Pinus* L., **Piscidia* L., **Pithecellobium* Mart., *Platymiscium* Vogel, ***Poaceae*, **Prosopis* L., **Pseudosmodium* Engl., **Psychotria* L., *Purshia* DC. ex Poir., **Quercus* L., **Rauwolfia* Cothen, **Rhamnus* L., **Rhus* L., *Rondeletia* L., *Roseodendron* Miranda, possibly **Salicornia* L. (as *chenoam), *Salvia* L., **Sapindus* L., **Sapium* Jacq., **Sarcobatus* Nees, **Sophora* L., **Tabebuia* Gomes ex DC., *Tabernaemontana* L., **Tetragastris* Gaertn., cf. **Tillandsia* L., **Tiquilia* Pers., *Vitex* L., *Yucca* L., **Zamia* L., **Zanthoxylum* L. **Gallery/riparian forests:** **Populus* L., **Salix* L.

SOUTH AMERICA

Including cerrado/caatinga, Patagonian steppe; some overlap with drier phases of the lower to upper montane broad-leaved forest: **Acacia*, **Acnistus* Schott, *Agave*, **Aspidosperma* Mart. & Zucc., ***Asteraceae* (Mutisioideae–Carduoideae affinities, Middle Eocene, 47.5 Ma, northwest Patagonia, Barreda et al., 2010), possibly *Atriplex* (as **chenoam), **Attalea* Kunth, *Barnadesia* Mutis ex L. f.,

Bejaria, **Berberis*, *Bolax* Comm. ex Juss., *Bonnetia* Mart., *Bowdichia* Kunth, *Bromelia*, **Brosimum*, *Bulnesia* Gay, **Bursera*, **Byrsonima*, Cactaceae (*Armatocereus* Backeb., **Cereus*, **Opuntia*, *Oreocereus* (A. Berger) Riccob., **Pereskia*, *Trichocereus* (A. Berger) Riccob.), **Caesalpinia*, *Cantua* Juss. ex Lam., **Capparis*, *Casearia*, **Castela* Turpin, *Castilla* Cerv., **Cavanillesia* Ruiz & Pav., **Cedrela*, **Ceiba* Mill., *Centrolobium* Mart. ex Benth., *Cercidium*, **Chlorophyllum* Liais, *Chrysobalanus* (family ***Chrysobalanaceae*, Pliocene), *Chiquiraga* Juss., *Clusia* L., *Colliguaja* Molina, *Copaifera*, *Copernicia* Mart. ex Endl., **Cordia* L., **Croton*, **Curatella*, ***Cyperaceae* (*Bulbostylis* Kunth, *Hypolytrum* Pers., *Scleria* P. J. Bergius), **Didymopanax* Decne. & Planch., **Dodonaea* Mill., **Drimys* J. R. Forst. & G. Forst., *Duranta* L., *Empetrum* L., **Enterolobium*, **Ephedra*, *Eriotheca* Schott & Endl., **Erythrina* L., *Euphrona* Vell., *Fabiana* Ruiz & Pav., *Gallesia* Casar., *Geoffraea* L., **Guaiacum* L., **Guarea* F. Allam. ex L., **Gunnera* L., *Hesperomeles* Lindl., *Hypericum* L., **Hyptis* Jacq., *Junellia* Moldenke, **Kielmeyera* Mart. ex Zucc., *Lampayo* F. Phil. ex Murillo, **Larrea*, *Lippia* L., **Lomatia* R. Br., **Loxopterygium* Hook. f., **Machaerium* Pers., **Maximiliana* Mart. (type, Pliocene), *Maytenus* Molina, **Mimosa*, *Monvillea* Britton & Rose, *Nassauvia* Comm. ex Juss., *Oreocallis* R. Br., **Ouratea* Aubl., *Palicourea* Aubl., *Pernettya* Gaudich., **Phyllanthus*, *Phytelephas* Ruiz & Pav., *Platymiscium*, ***Poaceae* (*Axonopus* P. Beauv., *Spartina* Schreb., *Trachypogon* Nees), *Poulsenia* Eggers, **Pouteria* Aubl., *Pradosia* Liais, **Prosopis*, **Pseudobombax* Dugand, **Rauwolfia*, **Roupala* Aubl., *Samanea* (Benth.) Merr., **Schinopsis* Engl., **Senecio* L. (widespread), **Smilax* L., **Spondias* L., **Stillingia* L., **Tabebuia*, *Thibaudia* Ruiz & Pav. ex J. St.-Hil., **Tillandsia*, *Vallesia* Ruiz & Pav., **Vantanea* Aubl., **Vochysia* Aubl., **Welwitschiaceae* (Cretaceous, Brazil), **Zanthoxylum*, **Ziziphus* Mill.

GALLERY/RIPARIAN FORESTS (E.G., THROUGH THE GRAN CHACO)

Arecastrum (Drude) Becc., *Albizia* Durazz., *Banara* Aubl., *Croton*, **Enterolobium*, **Ficus* L., *Geoffroea* Jacq., *Hexachlamys* O. Berg, *Holocalyx* Micheli, **Inga* Mill., **Nectandra* Rol. ex Rottb., *Patagonula* L., **Peltophorum* (Vogel) Benth., *Peschiera* A. DC., *Phytolacca* L., **Pisonia* L., **Ruprechtia* C. A. Mey., *Sorocea* A. St.-Hil., **Trichilia* P. Browne; **riparian widespread:** **Salix*, **Schinus* L.; **monte:** **Acacia*, *Atamisquea* Miers ex Hook. & Arn., **Caesalpinia*, **Celtis*, *Cercidium* (e.g., Quaternary, Mexico), *Condalia*, **Larrea*, **Mimosa*, *Prosopis* (e.g., Quaternary, Mexico), **Ziziphus*.

GRASSLAND

***Poaceae*; *Pariana* Aubl. (no annulus around pore on pollen), some phytoliths, and **Zea* L. (large size of pollen) identifiable to *genus, others only to **family.

MANGROVE

Acrostichum* L., **Avicennia* L., *Conocarpus* L., *Hibiscus* L. (pollen identifiable as **Hampea* Schltdl.–*Hibiscus*), **Laguncularia* C. F. Gaertn., **Nypa* Steck (as †Spinozonocolpites*; extinct in the New World after the Eocene), **Pelliceria* Planch. & Triana (southern Central America, northern South America; not presently known from Mexico or the Antilles), **Pterocarpus* Jacq. (e.g., Plio-Pleistocene, El Salvador), **Rhizophora* L.

SOUTH AMERICA

Genera above and **Crenea* Aubl. and **Pelliceria* Planch. & Triana.

BEACH/STRAND/DUNE

Achyranthes, *Batis* P. Browne, *Bontia* L., **Bucida* L., *Byrsonima*, Cactaceae (*Melocactus* Link & Otto, *Pilocereus* Lem.–*Cephalocereus*), *Canavalia* Adans., *Catesbaea* L., possibly *Suaeda* (as **chenoam), *Chrysobalanus*, *Cnidoscolus* Pohl, **Coccoloba*, *Colubrina* Rich. ex Brongn., **Comocladia*, **Cordia*, **Dodonaea* Mill., *Erithalis* P. Browne, *Ernodea* Sw., **Euphorbia*, **Guettarda*, *Gymnanthes* Sw., *Heliotropium* L., **Hibiscus* (microfossils as **Hampea* Schltdl.–*Hibiscus*), *Hippomane* L., *Ipomoea*, **Iresene* (chenoam, pollen of genus recognizable), *Jacquinia* L., *Lantana* L., **Manilkara* Adans., **Metopium* P. Browne, *Pectis* L., *Phyllanthus*, *Phyllostylon* Capan. ex Benth. & Hook. f., ***Poaceae* (*Cenchrus* L., *Uniola* L.), *Portulaca* L., *Rachicallis* DC., *Randia* L., **Reynosa* Griseb., *Scaevola* L., *Sesuvium* L., *Suriana* L., *Thespesia* Sol. ex Corrêa; **primarily present in other habitats but extending into the beach/strand/dune community:** **Acacia*, **Caesalpinia*, **Caesaria*, **Capparis*, **Coccoloba*, **Dalbergia* L. f., **Drepanocarpus* G. Mey., *Eugenia* (pollen identifiable as **Eugenia*/*Myrcia*, with other genera of the family having similar pollen), **Iresine*, **Laguncularia*, *Malache* B. Vogel, *Piscidia*, *Terminalia* L. (pollen identifiable as **Combretum* Loeff./**Terminalia*), **Tournefortia* L., *Ximenia* L.

FRESHWATER HERBACEOUS BOG/MARSH/SWAMP

This includes the pantanal. Some taxa are facultative aquatics, growing rooted in standing water. Some shrubs/trees may range into the swamp, but fully wooded swamps (**Nyssa* L., **Taxodium* Rich., **Tillandsia*; Asian **Glyptostrobos* Endl. as fossil in the New World) are included as a low, wet phase in the lower to upper montane broad-leaved forests.

Acoelorrhaphe* H. Wendl., *Ascyrum* L., **Bravaisia* DC., *Calathea* G. Mey., **Coccoloba*, *Coccothrinax* Sarg., *Cyperaceae* (**Carex* L., e.g., seeds, Pliocene, Alaska; *Cladium*, *Cyperus* L., *Eleocharis* R. Br., *Rhynchospora* Vahl, *Scirpus* L.), **Drosera* L., **Equisetum* L. (e.g., Cretaceous, Alaska; Alberta, Canada; Late Paleocene, Alberta, Canada), **Fraxinus* L., *Gerardia* Benth., **Heliconia* L., **Isoetes* L. (Late Paleocene, Alberta, Canada), Juncaceae (**Juncus* L.), *Lobelia* L., ***Poaceae* (*Paspalum* L., *Phragmites* Adans.), **Polygonum* L., **Sabal* Adans., **Sagittaria* L., **Sphagnum* L., **Typha* L., *Valisneria* Scop., **Vicia* L.

AQUATIC

Many putative taxa (*) occur in the Cretaceous and Paleocene; see, e.g., ***Haloragaceae*.

Azolla* Lam. (Cretaceous, Argentina; Paleocene, Alberta, Canada, Hoffman & Stockey, 1999), *Brasenia* Schreb., **Cabomba* Aubl., *Cabombaceae* (*†*Brasenites*, Cretaceous, Kansas, Wang & Dilcher, 2006), **Ceratophyllum* L. (Cretaceous, Mexico, Estrada-Ruiz et al., 2009), **Ceratopteris* Brongn., ***Cyperaceae* (*Eleocharis*), **Decodon* J. F. Gmel. (Cretaceous, Mexico, Estrada-Ruiz et al., 2009), *Eichhornia* Kunth, ***Haloragaceae* (as *†*Obispocaulis*, *†*Tarahumara*; Cretaceous, Mexico), **Hygrophila* R. Br., *†*Iara* (family unknown, Cretaceous, Argentina, Fanton et al., 2006), *Lemna* L., ***Lemnaceae*/***Araceae* (*†*Limnobiophyllum*, Paleocene, Alberta, Canada, Stockey et al., 1997; Hoffman & Stockey,

1999), *Limnocharis* Bonpl., **Ludwigia* L., **Myriophyllum* L., *Najas* L., **Nelumbo* Adans., **Nuphar* Sm., **Nymphaea* L., ****Nymphaeaceae** (**†Aquatifolia*, Cretaceous, Kansas, Wang & Dilcher, 2006), **†Nymphoides* Ség., **Pachira* Aubl., **†Paranymphaea* (fossil, Paleocene, Argentina; Saskatchewan, Canada), **Pistia* L. (Paleocene, Saskatchewan, Canada), **†Pluricarpellatia* (nymphaealean, Cretaceous, Brazil, Mohr et al., 2008), ****Poaceae** (e.g., species of *Luziola* Juss., *Paspalum* L., floating mats, South America), **Polygonum*, *Pontederia* L., **Potamogeton* L., **Sagittaria*, **Salvinia* Ség., **Thalia* L., **Trapa* L. (Eocene, U.S.A., anything earlier probably belongs to **†Hemitrapa*, S. Graham, personal comm., 2011), **†Trapago* (syn. **†Quereuxia*, affinity unknown, Cretaceous, Alberta, Canada, Stockey & Rothwell, 1997; S. Graham, personal comm., 2011), **Utricularia* L., *Vallisneria* Cothen., *Victoria* Lindl. (South America); **salt-water marshes**: possibly *Salicornia*, *Suaeda* (as ****chenoams**).

LOWLAND NEOTROPICAL RAINFOREST

Several (**) are known from the Paleocene, where generic identifications of macrofossils are uncertain or where generic distinction among microfossils is difficult.

TROPICAL ELEMENTS PRESENTLY EXTENDING INTO THE UNITED STATES

Avicennia* L., *Conocarpus*, **Laguncularia* C. F. Gaertn., **Palmae**, **Rhizophora* L.

Atanikerdruk flora

This Paleocene flora was documented from Greenland by Boyd (1990, 1992).

**†Musophyllum* (now **†Musopsis*, Heliconiaceae–Musa-ceae–Strelitziaceae complex).

Castle Rock flora

This flora dates to 64.1 Ma, Colorado (Johnson & Ellis, 2002).

**Elaeocarpaceae*, **Lauraceae*, **Sterculiaceae*.

NORTH AMERICA (CANADA, UNITED STATES, MEXICO)/ANTILLES/CENTRAL AMERICA

****Actinidiaceae** (**†Parasaurauia*, Late Cretaceous, Georgia, Herendeen et al., 1999), **Aegiphila* Jacq., cf. **Aguilaria* Ducke, **Alchornea* Sw., **Allophylus* L., *Anthodiscus* G. Mey., **†Antrophyllum*, ****Arecaceae**, cf. **Astrocaryum* G. Mey., *Batocarpus* H. Karst., **Bernoullia* Oliv., ****Bombacaceae**, **Brosimum* Sw., *Calophyllum* L., **Campnosperma* Thwaites, *Caryocar* L., **Cavanillesia* Ruiz & Pav., **Cedrela*, **Ceiba*, cf. **Chamaedorea* Willd., *Chaunochiton* Benth., **Chomelia* Jacq., cf. **Cionosicyos* Griseb., **Combretum–Terminalia*, *Couratari* Aubl., **Crudia* Schreb., **Ctenitis* (C. Chr.) C. Chr., *Dialium* L., *Elaeis* Jacq., **Faramaea* Aubl., **Ficus*, **Guarea*, **Gustavia* L., cf. **Hiraea* Jacq., *Huberodendron* Ducke, ****Lauraceae** (**†Marmarthia*, Late Cretaceous/Late Maastrichtian Hell Creek Formation, North Dakota, South Dakota, Montana, Johnson, 1996; **†Mauldinia*, Late Cretaceous, Georgia, Herendeen et al., 1999), **Lycopodium* L., **Matayba* Aubl., **Meliosma* Blume (Late Paleocene, Alberta, Canada, Hoffman & Stockey, 1999), *Minquartia* Aubl., **Ophioglossum* L., **Paragonia* Miers ex Bureau, *Parkia* R. Br., cf. **Paullinia* L., *Peltogyne* Vogel, ****Poaceae**, *Poulsenia*,

Prioria Griseb., cf. **Protium* Burm. f., **Pseudolmedia* Trecul., **Pteris* L., **Sapium*, **Selaginella* P. Beauv., **Spathiphyllum* Schott, **Sphaeropteris* Bernh.–*Trichipteris* C. Presl, *Swietenia* Jacq., **Symphonia* L. f., cf. **Tetrorchidium* Poepp., *Uribea* Dugand & Romero, **Vantanea*.

SOUTH AMERICA

There is an extensive record; see references in Graham (2010b).

Cerrejón flora

This flora dates to 58 Ma in Colombia (Wing et al., 2009).

Akania* Hook. f. (presently eastern Australia; Paleocene, Argentina), **Anacardium* L., **Anthurium* Schott, **Apeiba* Aubl., **Araceae**, ****Arecaceae**, **Asplundia* Harling, ****Asteraceae**, **Astrocaryum* G. Mey., **Blechnum* L. type, **Bombax* L., **Brownea* Jacq., **Callitriche* L., *Carapa* Aubl., **Carex*, **Casuarina* L., cf. **Catopsis* Griseb., *Catostemma* Benth., **Cecropia* Loefl., **Cedrela*, **Ceiba*, **Cochlospermum* Kunth, **Combretum–Terminalia*, cf. *Connarus* L., **Cordia*, **Coussapoa* Aubl., **Crescentia* L., **Crudia*, **Cyclanthus* Poit. ex A. Rich., **Ecclinusa* Mart., **Elatine* L., **Eleocharis*, **Erythrina*, *Eschweilera* Mart. ex DC., *Euterpe* Mart., cf. **Evodianthus* Oerst., ****Fabaceae**, **Ficus*, *Geonoma* Willd., **Gunnera*, **Heliconia*, **Humiriastrium* (Urb.) Cuatrec., **Hymenophyllum* Sm., **Ilex*, **Inga*, *Iryanthera* (A. DC.) Warb., **Jamesonia* Hook. & Grev., **Juncus*, **Lacmellea* H. Karst., ****Lauraceae**, *Licania* Aubl., **Lomariopsis* Fée, **Lophosoria* C. Presl., **Lycopodium*, **Lygodium* Sw., **Machaerium*, **Macoubea* Aubl., **Macrolobium* Schreb., ****Malvaceae**, **Manicaria* Gaertn., *Mauritia* L. f., ****Menispermaceae**, *Montrichardia* Crueg., **Ochroma* Sw., **Pachira* Aubl., **Parinari* Aubl., *Parkia* R. Br., *Pentaclethra* Benth., **Peumus* Molina, ****Poaceae**, cf. **Polygonum*, **Psittacanthus* Mart., **Pteris*, **Pterocarpus*, *Scheelea* H. Karst., **Schinopsis*, **Selaginella*, **Swartzia* Schreb., **Symphonia*, **Tabebuia*, *Vatairea* Aubl., **Vochysia*, *Warszewiczia* Klotzsch; **várzea**: **Alchornea*, **Anacardium*, **Astrocaryum*, *Calophyllum*, *Carapa*, *Cedrelinga* Ducke, **Ceiba*, **Cordia*, **Crudia*, *Euterpe*, **Ficus*, **Guarea*, **Hernandia* L., *Hura* L., **Luehea* Willd., **Macrolobium* Schreb., **Manicaria*, *Maquira* Aubl., **Mauritia* L. f., **Ocotea* Aubl., *Oenocarpus* Mart., *Phytelephas*, **Pithecellobium*, *Platymiscium*, ****Poaceae** (e.g., **Echinochloa* P. Beauv.), **Pseudobombax*, *Raphia* P. Beauv., **Rheedia* L., **Sapium*, cf. **Scirpus*, **Selaginella*, **Socratea* H. Karst., **Sphagnum* L., **Sterculia* L., **Thoracocarpus* Harling, *Triplarina* Raf., *Vatairea* Aubl., **Virola*, *Warszewiczia*, *Xylopia* L., **Xyris* L.; **Atlantic forest**: *Arapatiella* Rizzini & A. Mattos, *Buchenavia* Eichler, **Dicksonia* L'Hér., **Podocarpus* Labill.; **also cultivated and/or harvested**: **Araucaria* Juss., **Astronium*, **Caesalpinia*, **Cedrela*, **Dalbergia*, *Dialium*, *Diploon* Cronquist, **Drimys*, **Ecclinusa*, *Eriotheca*, *Eschweilera*, *Hevea* Aubl., **Ilex*, *Licania*, **Luehea*, **Manilkara*, **Nectandra*, **Ocotea*, **Paullinia*, *Plathymenia* Benth., *Simira* Aubl., *Sprucella* Stephani, *Theobroma* L., **Virola*.

LOWER TO UPPER MONTANE BROAD-LEAVED FOREST

In Latin America, this includes cloud forests, elfin forests, ceja, and some gymnosperm/conifer enclaves; many putative identifications for genera and families (*, **) are Late Cretaceous and Paleocene.

**Acer* L., **Adiantum* L. (Cretaceous, Argentina), **Aetanthus* (Eichler) Engl., **Alfaroa* Standl.–*Oreomunnea* Oerst.,

Alchornea*, **Allophylus*, **Alnus* Mill., **Alsophila* R. Br., **Araucaria* (Cretaceous, Mexico), *Arecaceae*, ***Asteraceae*, **Astrocaryum*, *cf. *Banisteriopsis* C. B. Rob., **Bauhinia* L., **Befaria* Mutis ex L., **Bernardia* Houst. ex Mill., **Blechnum* (Cretaceous, Argentina), **Bombax*, **Brunellia* Ruiz & Pav., **Bucida*, **Bursera*, **Caesarea* Cambess., **Calophyllum*, **Carapa*, **Carpinus* L., **Catostemma* Benth., **Cavanillesia* Ruiz & Pav., **Cecropia* (secondary, widespread), **Cedrela*, **Ceiba*, **Ceratozamia* Brongn., **Chamaedorea*, **Charianthus* D. Don., ***chenoam* (**Iresine*), **Chlorophyllum*, **Chrysophyllum* L., **Clethra* L., **Cleyera* Thunb., **Clusia* L., **Coccoloba*, **Cordia*, **Cornus* L., **Cosmibuena* Ruiz & Pav., **Cupania*, **Cupressus* L., **Cyathea* Sm., **Cymbopetalum* Benth., **Cyrilla* Garden ex L., **Dacrydium* Lamb. (Cretaceous, Argentina), **Dacryodes* Vahl–*Sloanea* L. (low-altitude wet forests, Antilles), **Danaea* Sm., **Daphnopsis*, **Dendropanax* Decne. & Planch., **Dennstaedtia* Bernh. (Cretaceous, Argentina), **Desmanthus* Willd., **Dichapetalum* Thouars, **Didymopanax*, **Dioscorea* L. type, **Diospyros* L., cf. **Doliocarpus* Rol., **Drimys*, **Dryopteris* Adans. (Cretaceous, Argentina), ***Ericaceae* (**Cavendishia* Lindl. type), **Erythrina* L. (widespread), **Eucommia* Oliv. (extinct in the New World), **Eugenia* (as **Eugenia*–*Myrcia*), **Euterpe*, ***Fagaceae* (*†*Quercinium*, Cretaceous, Mexico), ***Fagaceae* s.l. (*†*Antiquacupula*, *†*Protofagacea*, Cretaceous, Georgia, Herendeen et al., 1999), **Fagus* L., **Faramea*, **Ficus* (widespread), **Freziera* Willd., **Gaussia* H. Wendl., **Gleichenia* Sm. (Cretaceous, Argentina), cf. **Glycydendron* Ducke, **Grammitis* Sw., **Guarea*, **Guazuma* Mill., **Gustavia* L., ***Hamamelidaceae* (*†*Allonia*, Cretaceous, Georgia, Herendeen et al., 1999), **Hampea*/Hibiscus, **Hauya* DC., **Hedyosmum* Sw., **Heliconia*, **Hemitelia* R. Br.–*Cnemidaria* C. Presl, **Hiraea*, **Hymenaea*, **Hymenophyllum* (Cretaceous, Argentina), **Ilex*, **Jacaranda*, **Jamesonia*/Eriosorus Fée complex, ***Juglandaceae* (as *†*Monopites* fossil pollen, referable to *Alfaroa*, *Engelhardia* Lesch. ex Blume, *Oreomunnea* type), **Juglans* L., **Justicia* L., **Lacmellea*, **Laetia*, ***Lauraceae* (**Persea* type, Cretaceous, Mexico), **Laurelia* Juss. (Cretaceous, Argentina), **Liquidambar* L., **Lisianthus* L., **Lomariopsis*–*Stenochlaena* J. Sm., **Lonchocarpus* Kunth, **Lophosoria*, **Luehea*, **Lycopodium*, **Lygodium*, **Magnolia* L., **Malpighia* L., ***Malvaceae* (as *†*Javelinoxylon*, Cretaceous, Mexico), **Manicaria* type, **Marcgravia* L., **Mastichodendron* (Engl.) H. J. Lam, **Matayba*, ***Melastomataceae*, **Meliosma*, **Mimosa*, **Mortoniendendron* Standl. & Steyerl., **Myrcia*, **Myrica* L., **Norantea* Aubl., **Ocotea*, **Oreopanax* Decne. & Planch., **Ormosia* Jacks., **Ostrya* Scop., **Paullinia*, **Peltophorum*, **Peperomia* Ruiz & Pav., **Perrottetia* Kunth, **Persea*, **Petrea* L., **Pinus*, **Pityrogramma* Link, ***Platanaceae* (Early Paleocene Castle Rock flora), **Platanus* L., **Pleodendron* Tiegh., ***Poaceae*, ***Podocarpaceae*–*Taxodiaceae* affinities (Cretaceous, Mexico), **Podocarpus* (Cretaceous, Argentina), **Populus*, **Posoqueria* Aubl., cf. **Pouteria*, **Prestonia* R. Br., **Protium*, **Prunus* L., **Pseudobombax*, **Psidium* L., **Psilotum* Sw., **Psychotria*, **Pteridium* Gled. ex Scop., **Pteris*, **Quercus* L., **Rajania* L., **Rauwolfia* Ruiz & Pav., **Rhamnus*, **Richeria* Vahl, **Roupala* Aubl., **Rourea* Aubl., **Roystonea* O. F. Cook, **Rubus* L., **Sabicea* Aubl., **Salix*, **Samanea* (Benth.) Merr., **Sambucus* L., **Sapium*, **Scheelea*, **Securidaca* L., **Selaginella*, **Serjania* Mill., **Smilax*, **Spathelia* L., **Spathiphyllum*, **Sphaeropteris*/Trichopteris, **Stillingia*, **Struthanthus* Mart., **Styrax* L., **Symphonia*, **Symplocos*, **Synechanthus* H. Wendl. type, **Tapirira* Aubl., **Tecoma* Juss., **Terminalia* (as **Combretum*–*Terminalia*), **Ternstroemia* Mutis ex L. f. (as *†*Ternstroemites*, Early Eocene, North Dakota, U.S.A.), **Tetragastris*,

Tetrorchidium* Poepp., **Thyrsopteris* Kunze (Cretaceous, Argentina), **Ticodendron* Gómez-Laur. & L. D. Gómez (as *†*Ferrignocarpum*), **Tilia* L., *Tiliaceae* (Early Paleocene Castle Rock flora), cf. **Tillandsia*, **Tontelea* Miers., **Tournefortia*, **Trithrinax* Mart., **Ulmus* L., **Weinmannia* L., **Zanthoxylum*; **open, secondary, clearings:** **Alibertia* A. Rich. ex DC., **Borreria* G. Mey., **Byttneria* Loeffl., **Cuphea* P. Browne, **Desmanthus*, **Dicranopteris* Bernh., **Passiflora* L., ***Poaceae*, **Rajania* L., **Smilax* L.

SOUTH AMERICA/ANTARCTICA

This includes tropical elements extending into the Andean forest belts; many (*, **) identifications are Late Cretaceous and Paleocene.

Acalypha* L., **Acmopyle* Pilg. (Cretaceous, Argentina, Chile), **Adiantum*, **Alchornea*, **Alnus*, **Alsophila*, **Anemia* Sw., **Athyrium* Roth, **Antrophyum* Kaulf., **Araucaria*, *Araucariaceae* (Cretaceous, Antarctica; **Araucaria*, *†*Araucarites*, foliage, Falcon-Lang & Cantrill, 2001; *†*Araucarioxylon*, *†*Araucariopsis*, wood), **Asplenium* L., ***Asteraceae*, **Austrocedrus* Florin & Boutelje, **Blechnum*, **Bocconia* L., **Bolax*, **Bonnetia*, **Botrychium* Sw., **Bravaisia*, **Brocchinia* Schult. f., **Brunellia*, **Calophyllum*, **Cedrela*, **Chrysophyllum*, **Clethra*, **Clusia*, **Cnemidaria*–*Hemitelia*, **Ctenis*, **Dacrydium*, **Dennstaedtia*, **Dicksonia*, **Dicranopteris* Bernh., **Drimys*, **Dryopsis* Holttum & P. J. Edwards, **Empetrum*, **Escallonia* Mutis ex L. f., **Euterpe*, **Ficus*, **Fitzroya* Hook. f. ex Lindl., **Gleichenia*, **Guettarda*, **Gunnera*, **Gyranthera* Pittier, **Hedyosmum*, **Heliamphora* Benth., **Heliconia*, **Helicarpus* L., **Ilex*, ***Isoetaceae*, **Isoetes*, **Juglans*, **Laplacea* Kunth, **Lecythis* Loeffl., **Libocedrus* Endl., **Lippia*, **Lonchocarpus*, **Maytenus*, **Meliosma*, **Miconia* Ruiz & Pav., **Mora* Benth., **Murraya* J. König ex L., **Myrica*, **Nephrolepis* Schott, **Nothofagus* Blume (Cretaceous, Argentina), **Ocotea*, **Oreopanax*, **Osmunda* L., **Palicourea*, *†*Pecopteris* Brogn., **Pernettya*, **Persea*, ***Poaceae*, **Podocarpus* (Cretaceous, Argentina, as *†*Podocarpidites*, *†*Gamerroites*), **Polystichum* Roth, **Protium*, **Prunus*, **Psychotria*, **Pterocarpus*, **Rhus*, **Sacoglottis* Mart., **Salix*, **Sambucus*, **Saurauia* Willd., **Sloanea*, **Stegolepis* Klotzsch ex Körn., **Styrax*, **Symplocos*, **Tabebuia*, **Talauma* Juss., ***Taxodiaceae* (Middle Cretaceous, Antarctica, *†*Athrotaxites*, foliage, Falcon-Lang & Cantrill, 2001; *†*Taxodioxylon*, wood), **Tibouchina* Aubl., **Toxicodendron* Mill., **Trema* Lour., **Trigonobalanus* Forman, **Turpinia* Vent., **Tyleria* Gleason, **Urtica* L., **Vaccinium* L., **Vantanea*, **Viburnum* L., **Weinmannia*, **Zamia*.

DECIDUOUS FOREST

This refers to plant communities in eastern North America, mixed with riparian and coniferous forest in western North America.

Acer* (fruits, Cretaceous, Kirk Johnson locality, Hell Creek Formation, South Dakota, see Renner et al., 2008: 798), cf. *†*Acer arcticum* (Late Paleocene, Alberta, Canada, Sapindaceae, Hoffman & Stockey, 1999), *†*Alismaphyllites* (Late Paleocene, Alberta, Canada, *Alismataceae*, Hoffman & Stockey, 1999), **Alnus* Mill. (Dillhoff et al., 2005), *†*Amersinia* (Late Paleocene, Alberta, Canada, ***Cornaceae*, Hoffman & Stockey, 1999), **Andromeda* L. (e.g., Cretaceous, Greenland), **Asimina* Adans., ***Asteraceae*, *†*Averrhoites* (Late Paleocene, Alberta, Canada, extinct, ***Oxalidaceae*, Hoffman & Stockey, 1999), *†*Beringiaphyllum* (Late Paleocene, Alberta, Canada, ***Cornaceae*, Hoffman & Stockey, 1999), **Betula* L. (Dillhoff et al., 2005), **Carpinus*–*Ostrya* (Dillhoff et al., 2005, pollen),

**Carya* Nutt. (putative, Dillhoff et al., 2005), **Castanea* Mill., **Chaetoptelea* Liebm. (Late Paleocene, Alberta, Canada, Hoffman & Stockey, 1999), **Chamaecyparis* Spach, **Cornus*, **Dennstaedtia* (Late Paleocene, Alberta, Canada, Hoffman & Stockey, 1999), *†*Deviacer* (Late Paleocene, Alberta, Canada, **Sapindaceae, Hoffman & Stockey, 1999), **Diospyros* L. (Cretaceous, Greenland), **Fagus*, **Fraxinus*, **Ginkgo* L. (Cretaceous, Alberta, Canada; Late Paleocene, Alberta, Canada, Hoffman & Stockey, 1999), **Gleditsia* L., **Glyptostrobus* (Cretaceous, Alberta, Canada; Late Paleocene, Alberta, Canada, Hoffman & Stockey, 1999), **Ilex*, *†*Joffrea* (Late Paleocene, Alberta, Canada, related to modern **Cercidiphyllum* Siebold & Zucc., Hoffman & Stockey, 1999), **Juglans* (Dillhoff et al., 2005), **Larix* Mill., cf. *†*Lemnospermum* (Late Paleocene, Alberta, Canada, **Araceae), **Lindera* Thunb., **Liquidambar*, **Liriodendron* L., *†*Macginicarpa* (Late Paleocene, Alberta, Canada, **Platanaceae, Hoffman & Stockey, 1999), **Magnolia* (Cretaceous, Greenland), **Metasequoia* Hu & W. C. Cheng (Cretaceous, Alberta, Canada; Late Paleocene, Alberta, Canada, Hoffman & Stockey, 1999), **Nyssa*, **Osmunda* (Upper Cretaceous; Late Paleocene, Alberta, Canada, Hoffman & Stockey, 1999), **Pinus*, **Platanaceae (*†*Erlinghorfia*, *†*Platanites*, Johnson, 1996, Late Cretaceous/Late Maastrichtian Hell Creek Formation, North Dakota, South Dakota, Montana), *†*Platananthus* (Late Paleocene, Alberta, Canada, **Platanaceae, Hoffman & Stockey, 1999), **Platanus* (Late Paleocene, Alberta, Canada, Hoffman & Stockey, 1999), **Poaceae, **Populus*, **Pterocarya* Kunth (Dillhoff et al., 2005), **Quercus* (Dillhoff et al., 2005), **Salix*, **Taxodium*, **Tilia*, **Ulmus* (Early Middle Eocene, British Columbia, Canada, Dillhoff et al., 2005), *†*Zingiberopsis* (Late Paleocene, Alberta, Canada, Zingiberaceae, Hoffman & Stockey, 1999).

NORTHERN TEMPERATE ELEMENTS IN MID-ALTITUDE EASTERN MEXICO

**Abies* Mill., **Acer*, **Alnus*, **Carpinus*, **Cornus*, **Diospyros*, **Fagus*, **Ilex*, **Juglans*, **Liquidambar*, **Lycopodium*, **Magnolia*, **Myrica*, **Ostrya*, **Pinus*, **Platanus*, **Populus*, **Prunus*, **Pteridium*, **Quercus*, **Rubus*, **Salix*, **Sambucus*, **Smilax*, **Ulmus*.

WARM-TEMPERATE ELEMENTS WITH NORTHERN TEMPERATE ELEMENTS IN MID-ALTITUDE EASTERN MEXICO

**Alfaroa* (as **Alfaroa–Oreomunnea*), **Clethra*, **Cyathea*, **Drimys*, **Eugenia* (pollen as **Eugenia–Myrcia*), **Hedyosmum*, **Heliconia*, **Meliosma*, **Peperomia*, **Persea*, **Podocarpus*, **Weinmannia*.

CONIFEROUS FOREST

BOREAL CONIFEROUS FOREST

**Abies*, **Alnus*, **Betula* (family Betulaceae and genus from several sites in northern North America; see Graham, 1999: 162–233; oldest records are from Middle Eocene Allenby Formation, British Columbia, Canada; Crane & Stockey, 1987), **Larix*, **Picea* A. Dietr., **Pinus*, **Populus*, **Salix*, **Sphagnum*, **Thuja* L., **Tsuga* (Endl.) Carrière.

WESTERN MONTANE/ALPINE CONIFEROUS FOREST

Many putative identifications (*, **) have come together for the first time in the Middle Eocene of northwestern North America.

Abies* (Dillhoff et al., 2005), **Acer*, **Alsophila*, **Aphanactis* Wedd., **Asteraceae, **Berberis*, **Buddleja* L., **Castanopsis* (D. Don) Spach, **Catopsis*, **Ceanothus*, **Cercocarpus*, **Chamaecyparis*, **Cornus*, **Crataegus*, **Cupressus*, **Cyathea*, **Drimys*, **Ericaceae (Arbutus*, **Arctostaphylos*, **Menziesia* Sm., **Pernettya*, **Rhododendron* L.), **Garrya* Douglas ex Lindl., **Holodiscus*, **Juniperus*, **Libocedrus*, **Mahonia*, **Myrcia* (pollen as **Eugenia–Myrcia*), **Oreopanax*, **Oxylobus* (DC.) Moc. ex A. Gray, **Picea* (modern distribution to the mountains of northern Mexico; fossils to Veracruz, Mexico, and Guatemala in the Neogene, Dillhoff et al., 2005), **Pinus* (Dillhoff et al., 2005), **Poaceae, **Podocarpus*, **Prunus*, **Pseudotsuga* Carrière, **Quercus*, **Ribes* L., **Sequoia* Endl., **Smilax*, **Tsuga* (Dillhoff et al., 2005); **moist/riparian:** **Alnus*, **Betula*, **Clethra*, **Cornus*, **Fraxinus*, **Ilex*, **Juglans*, **Oreopanax*, **Phoradendron* Nutt., **Platanus*, **Polypodium* L., **Populus*, **Prunus*, **Psittacanthus* Mart., **Salix*, **Struthanthus*, **Styrax*, **Symplocos*, **Tillandsia*, **Umbellularia* (Nees) Nutt., **Xylosma* G. Forst.; **highlands:** **Artemisia* (lower elevations), **Calocedrus* Kurz/**Libocedrus*, **Cupressus*, **Cyperaceae, **Ericaceae (**Gaultheria* L., **Kalmia*, **Rhododendron*, **Vaccinium*), **Erigeron* L., **Picea*, **Pinus*, **Poaceae, **Prunus*, **Pseudotsuga*, **Sequoiadendron* J. Buchholz, **Sphagnum* (upper elevations), **Taxus* L., **Thuja*, **Tsuga*.

APPALACHIAN CONIFEROUS FOREST

Abies*, **Betula*, **Ericaceae (Rhododendron*), **Picea*, **Pinus*.

GULF COASTAL (PINE) CONIFEROUS FOREST

**Pinus*.

PINE-OAK (MEXICO) CONIFEROUS FOREST

**Alnus*, **Cuphea*, **Juglans*, **Pinus*, **Populus*, **Quercus*, **Struthanthus*.

ALPINE TUNDRA/PÁRAMO

Many putative taxa (*) are from the Pliocene and Quaternary.

NORTH AMERICA/ANTILLES/CENTRAL AMERICA

Arenaria* L., **Asteraceae, **Cerastium* L., **Cirsium* Mill., **Draba* L., **Eryngium* L., **Gnaphalium* L., **Juncaceae (Luzula* DC.), **Lupinus* L., **Oxylobus*, **Phacelia* Juss., **Plantago* L. (e.g., Late Pliocene, Alaska), **Poaceae, **Potentilla* L., **Puya* Molina, **Ranunculus* L. (Quaternary records, and in the Pliocene of Colombia), **Senecio* (possibly among some pollen identified as *Asteraceae/Compositae).

SOUTH AMERICA (INCLUDING SHRUBBY PLANTS OF THE PUNA)

Acaena* Mutis ex L., **Arenaria*, **Asteraceae, **Azorella* Lam., **Baccharis*, **Buddleja*, **Calceolaria* L., **Cyperaceae, **Distichia* Nees & Meyen., **Draba* (North America), **Escallonia*, **Espeletia* Mutis ex Bonpl., **Fuchsia* L., **Gaultheria* L., **Gentiana* L., **Gynoxys* Cass., **Hedyosmum*, **Hypericum*, **Jamesonia*, **Lupinus*, **Miconia*, **Montia* L., **Plantago*, **Poaceae (Aciachne* Benth., **Calamagrostis* Adans., **Chusquea* Kunth [including **Swallenochloa* McClure], **Deyeuxia*

Clarion ex P. Beauv., *Festuca* L., *Jarava* Ruiz & Pav., *Stipa* L.), **Polylepis* Ruiz & Pav., *Puya*, **Rhizocephalum* Wedd., *Senecio*, **Weinmannia*.

TUNDRA

Many reports (*) are from the Pliocene and Quaternary.

NORTH AMERICA

Isolated clusters of **Abies* and **Picea*, dwarf **Alnus*—**Betula*—**Salix*, ***Asteraceae*, ***Cyperaceae* (**Carex*, *Eriophorum* L., *Luzula*), *Dryas* L., *Empetrum*, ***Ericaceae* (**Arctostaphylos*, *Cassiope* D. Don, *Ledum* L., **Loiseleuria* Desv./*Rhododendron*, **Vaccinium*), **Hippuris* L., *Menyanthes* L., ***Poaceae*, **Potentilla*, **Rubus*, *Saxifraga* L., *Silene* L.